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Portland State University

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HOST: Good evening, ladies and gentlemen. On behalf of the Oregon State System of Higher Education and Portland State University, I am pleased to welcome you to the 26th lecture in the Condon lecture series. Many of you I know are familiar with the history of this series of lectures, but for those of you who are not, let me trace briefly its background. The series was established by the State Board of Higher Education in 1943 in recognition of the scholarly achievements of Thomas Condon, the first chairman of the Department of Geology at the University of Oregon. It was Dr. John C. Merriam, former president of the Carnegie Institute, who prevailed upon the board to establish the lectureship to increase the awareness of human values in science and nature.

Thomas Condon, for whom the lectureship is named, was, in his early career, a Congregational missionary. After spending some 10 years in western Oregon, he moved to The Dalles in 1868. And during his 13 years there, in eastern Oregon, his interest was attracted by the variety of rocks and the fossils that they contained. His efforts involved the collection of specimens and their identification, this often involving shipment to the east for authoritative identification. Much of Thomas Condon's collections are still today in eastern museums. Condon's work soon led to statewide recognition, and to his appointment as state geologist. When the University of Oregon was established in 1876, Condon was elected to the chair of natural sciences. And,

later, became the first chairman of the Department of Geology, a post which he held until his death.

Condon's impact was only in part a matter of his scientific contributions. In considerable measure, it was a matter of his unique talent for interpreting to the layman the results of his inquiries. Much of his effort was, in fact, devoted to this kind of activity. And it was a recognition of this accomplishment, as much as his contribution to science, that led Dr. Merriam to advocate the establishment of this series in Condon's name.

Since 1944, 25 eminent scientists have contributed to the series, in areas ranging from history and linguistics, to physics and mathematics. This year, the Condon Lecture Committee is pleased to present one of the foremost authorities in the field of animal behavior. Dr. Robert A. Hinde is professor of zoology and honorary director of the medical research unit on the development and interpretation of behavior at Cambridge University in England. Dr. Hinde was educated at Cambridge and Oxford, receiving his doctor of philosophy degree from Oxford in 1950. Among his many honors are his election as fellow of St. John's College, Cambridge, in 1958, and his appointment to a Royal Society research professorship in 1963. He is the author of a number of books, and has been a prolific contributor to a wide range of scientific journals. His lecture topic tonight, and tomorrow night, is the development of social behavior in primates. It is a pleasure, and an honor, to present to you Dr. Robert A. Hinde.

[applause]

DR. ROBERT A. HINDE: Well, I think that anybody who introduces the Condon lecture should really make the point that the Condon lecturer is awfully lucky to come on a trip like this, especially when he comes all the way from England, and gets the opportunity to meet a lot of his old friends again, and to make a number of new ones, and to get around and see a lot of nice places, and see a state he hasn't seen before. And the only snag about it is these wretched lectures he has to give.

[laughter]

Well now, in these two lectures, I'm going to argue that the study of the social behavior of animals can help, in certain ways which I shall try and specify in a moment, in the understanding of our own behavior. And in the time available to me, I'm going to have to select from among the many problems which I might discuss, and I shall make that selection partly on the basis of my own competence, and partly on the basis of what I think is important. And of course, what I think is important is a matter of opinion. And, all I would say on that issue is, that

if there is anybody here who does not agree that it is at least as important to try and understand our own behavior, as it is to try and understand, let's say, to take an example at random, how to drive cars across the moon, then, I hope they'll agree that at least the problems that I'm going to talk about are worth pursuing.

Now, my approach to the study of human behavior is that of a biologist. And I'm going to start off by saying a few words about what I see as the relevant characteristics of a biological approach to the study of behavior. The first point is, that the description and classification of biological phenomena is an essential first stage in their analysis. In the study of organisms, the work of generations of taxonomists and systematists was necessary before any progress could be made. And exactly the same is true of the study of behavior. You have to break up the continuous stream of behavior shown by an organism into elements; you must describe them, you must classify them, before you can make any progress in the analysis of the behavior. Philosophers of science, who, in my view, have too often started their lives as physicists, like to refer to this stage as natural history. With a sort of slight sneer in their voices. But it's just because the description of biological phenomena can never be complete, and therefore has to be selective, that it's important, because the way in which you select what you describe affects your subsequent theory.

The second point concerns the foreseeable goals which a biologist can set himself. In most of his work, the biologist can't hope for dramatic revelations. He's got to be content with attempting to make generalizations of rather limited scope. And I think this is peculiarly true in the study of behavior because the diversity of organisms in the world, and the diversity of behavior which each type of organism shows, means that every research finding must be, or should be, accompanied by statements of the limits of its generality. And one must remember that the broader the scope of the generalizations that one attempts to make, the less precise is the generalization likely to be. Notwithstanding the recent achievements of biology, biology is still a very long way from understanding all its subject matter in terms of a few fundamental particles. And I believe that humility in the face of diversity is a very essential part of a biologist's training.

The third point I want to make about the characteristics of the biological approach concerns the relations between levels of complexity. In biology, these are of two quite distinct sorts. First, as in all sciences, one can proceed by analyzing the more complex phenomena into its components and gain some degree of understanding of the more complex phenomena, in terms of the products of the analysis. So that you can break down complex sequences of behavior into individual responses, and you can break those down into muscle contractions, and you can understand those in terms of activity in the nervous system, and so on. This is an

analysis of causal chains; the animal behaves because the muscles contract, the muscles contract because of the nervous impulses, and so on. But within behavior itself, there are levels of complexity of a quite different sort, levels which you can characterize as ranging from reflexive to intelligent behavior, or as being typical of lower to higher phyla in the animal kingdom. Now, it's conceivable that the higher levels of this sort will eventually be understandable in terms of the same sorts of mechanisms that are responsible for the lower levels. But it's an error to think that the more complex phenomena consist of, or are caused by, the simpler ones. It's an error to make out, for instance, that intelligent behavior consists of reflexes. This was the error into which the Pavlovian school fell in its later days.

Now, I've forgotten to press the first button so if I press this twice… perhaps we'll see where we are. Given the tremendous differences that I've tried to emphasize between species, one's got to ask whether it's really likely that the study of animal behavior can contribute at all to the study of human behavior. And on the face of it, it seems improbable. The development of man's personality and the way in which he interacts with others depend on language, and they depend on a level of conceptual functioning which is of a quite different order from what one finds in any other species. Furthermore, it's very much influenced by man's social environment. And man has diverse social systems, any one of which is infinitely more complex than anything that's found in animals. So it's quite clear that biologists are not going to solve the problems of human personal relations. But I believe that if they maintain the humility in the face of diversity to which I just referred, they can make some contributions. And I think those contributions can be of four types.

First, the study of animal behavior can lead to the development of methods which are suitable also for the study of some aspects of human behavior. This applies especially to methods for describing and classifying behavior. I've already mentioned the importance of this in biology, but for a long time it was very much neglected in the study of human behavior. Recently, however, the techniques developed in the study of animal behavior are being applied with considerable success in such problems as the study of the behavior of nursery school children, the study of interactions between psychiatrists and their patients, and so on. This is a matter which I'm not going to discuss any further.

The second way in which studies of animal behavior may be relevant is in the examination of carefully delimited problems. Sometimes, perhaps simply because it's not ethical to do experiments with man, you must work with animals. And variables can be isolated which prove subsequently to be important in the human case. Now always, of course, generalization of research findings from animal to man must be made with the greatest caution, and wherever

possible, assessed against other sources of evidence. Now, I shall spend most of my second lecture discussing one particular topic of this sort.

The other two ways in which animal data are relevant to the human case are I think somewhat more intangible, but perhaps more important. Sometimes the study of animal behavior can be used to establish principles of behavior whose relevance to man can subsequently be assessed. And in this context, it's just because animals are different from man that they are useful. Their relative simplicity highlights theoretical issues, or permits the isolation of problems that might otherwise be shrouded in the complexity of the human case. Well now, this is of course a peculiarly dangerous procedure. And it's been grossly misused by certain recent popularizers, who by selecting facts to fit theories, neglecting awkward cases, and failing to distinguish firm fact from flight of fancy, have gone a long way towards reducing man to nothing but a naked ape. These dangers can, however, be circumvented. Fourth, the study of animal behavior can give perspective to the behavior of man, both emphasizing those features which he shares with lower forms, and pinpointing his uniqueness.

Well now, I believe that the study of social behavior and the development of social behavior is rather complicated. Now, every lecturer says this about his own subject matter; the difference is that in my case it happens to be true.

[laughter]

And for that reason, I'm going to spend a good deal of this evening, as it were, preparing the ground, because I think it's essential to get some of the conceptual issues straight, before one really digs down into the basic problems themselves. And in the second lecture, I shall focus attention on the specific problem of the development of social behavior in primates. Now the first thing one's got to think about is just what one means by social behavior. And it's usually—until recently it's had rather low status in the studies of behavior and especially animal behavior, for this reason—it's nearly always been studied in relation to one or another functional group of behavior patterns. Behavior to members of the other sex, in performation and sexual behavior, behavior between parents and offspring in parental and filial behavior, and so on. And it's even been implied that social behavior is merely a pacificatory label for all types of behavior involving other members of the species. Twenty years ago, Dr. Niko Tinbergen, who's one of the pioneers of modern studies of animal behavior, wrote: "There is, in my opinion, no social instinct. There are no special activities to be called 'social' that are not part of some other instinct." I should explain that instinct, in Dr. Tinbergen's terminology, was used with reference to the causal basis of behavior. Now, the sources of Tinbergen's view are of some interest. They arose, I think, in this way: much of the progress in the study of animal

behavior in recent years has come through the use of the relatively stereotyped species characteristic movement patterns, as identifiable markers in the stream of behavior shown by an animal. I'm referring here both to the sort of rather bizarre signal movements, like threat and courtship postures which animals use, and also to the more ordinary movements used in locomotion and various maintenance activities, which nevertheless are stereotyped within the species.

And the instinct theory of Konrad Lorenz, which was a powerful force in the development of modern studies of animal behavior, pivoted on these instinctive movements. Lorenz had a theory of motivation which was what we call an energy theory of motivation, it had much in common with the theories of Sigmund Freud and McDougall; and he believed that behavior is activated by an internal energy, Lorenz called it reaction-specific energy, Freud called it libido. And he believed that this energy was discharged in the performance of these stereotyped and instinctive movements. Now, it was primarily because there are no special movements that can be called social, which are not part of some other category of behavior, that Tinbergen argued that there's no social instinct. Since there were no special movements, and since instinctive behavior was thought to be brought to an end by the performance of special movements, there could be no social instinct.

Well, it's now known that sequences of behavior are brought to an end in a variety of ways, and perhaps the most important is by the reception of so-called consummatory stimuli, which the animal receives as a consequence of its behavior, not through the performance of movement, but through the reception of stimuli which the animal encounters as a result of those movements. For instance, bouts of feeding behavior are brought to an end through stimuli in the mouth, throat and stomach regions from the food, not through the discharge of energy in the act of eating. Another well-known example concerns the courtship of the three-spined stickleback. In this species, the male builds a nest, and then every egg-laden female that comes along he courts with a zig-zag dance, and then he leads her to the nest, where she lays her eggs, which he then fertilizes. And after he's fertilized the eggs, any more egg-laden females who come along, he doesn't court, but he attacks. And the question is, what causes the reduction in his readiness to court females? And at first thought you would think that it was the act of ejaculating sperm onto the eggs in the nest. Well, this was investigated by comparing the behavior of males which had or had not been allowed to court a female, which had or had not had a female in their nest, which had or had not fertilized a clutch in their nest, and which had or had not seen a clutch in their nest without fertilizing it. I should say smelled. Because it turned out that the only one of these things that produced a reduction in the male's tendency to court females, was the smell of eggs in the nest. The courtship behavior is brought to an end by the stimuli from the eggs encountered as a result of courtship. And so it's not the

performance of a particular act, but the perception of particular stimuli, which leads to the drop in motivation. By analogy, the fact that there are no special acts whose performance lowers social motivation, cannot be used as evidence against the view that social behavior, defined causally, is a discrete category, and Tinbergen's view that social behavior always depends on other instincts loses its force. If I could just have the lights up for a minute or two?

Now, in most social species, when an individual becomes separated from its companions, it shows a special type of searching behavior, which increases the probability that contact with them will be reestablished. And this searching behavior is switched off by consummatory stimuli indicative of the proximity of other members of the species. So that in this respect, social behavior is on a par with other types of behavior, like feeding. And it's thus possible, and indeed it's necessary, to regard social behavior as a category in its own right.

Now this raises a further problem. If social behavior is independent of other categories of behavior, to what extent may social relationships between individuals be independent of the particular types of behavior involved in their interaction? And again I'm going to start with Tinbergen's view that social behavior is in some sense part of other types of behavior. Tinbergen's view was in harmony with the view of a German student of animal behavior called von Uexküll who was writing in the twenties and thirties. He held that the social behavior in animals involved relationships of a *kumpan* type. Now the word *kumpan* in Germany doesn't mean exactly the same as *companion* in English; it refers to somebody who is a companion in a special type of activity. Like we say drinking companion or business colleague. And the implication is that the kumpanship is limited to one context. And Lorenz described, for instance, the behavior of one of his tamed jackdaws which he'd reared by hand, and the jackdaw used to treat him as its parent, it used to go off and feed with other jackdaws, and it used to court the house maid. Each category of behavior was directed towards a different individual.

Well now, that may happen, but it also happens that one individual is the preferred companion for many, or all activities. For example, an infant rhesus monkey may direct towards its mother filial behavior, grooming, soliciting for grooming, sexual presenting, aggressive behavior, play behavior, and so on. In other words, the individual characteristics of its mother become part of the adequate stimulus situations for a number of different patterns of behavior. So that in this sense, at least, the social relationship with the mother transcends the particular activities.

Now we come on to yet another problem. A relationship of that sort which transcends a number of different categories of behavior acquires other properties. In our own species, for instance, we might refer in colloquial speech to a relationship as having the quality of being affectionate. Now, it's not at all respectable for a biologist to talk about something like

affection. It's the sort of problem which is considered indecent and shuffled out of the way, because it's too intangible. I think that the difficulty with the concept of affection is that it's multidimensional, and attempts to measure affection along any one dimension are therefore bound to fail. But what we can do is at least attempt to specify those dimensions which are relevant. And human relationships are said to be affectionate, for instance, to the extent that one individual directs a variety of types of behavior towards one other individual, that the relationship is of long duration, and survives temporary absences, that the presence of the partner provides security in anxiety-provoking situations, that the behavior of each of the participants is ordered in relation to the ongoing behavior of the other, and so on.

Now, how relationships of this sort develop in the individual I believe to be one of the most important problems that—well, I am biased of course—but I think it's one of the most important problems that any scientist could look at. And I'm going to try and say a little bit about it tomorrow. The issue here is, that the quality of the relationship is not closely dependent on the particular motivational context. And many of the labels that we apply to the social behavior of our fellows, such as shy or self-assertive, are in fact relevant to a broad spectrum of context. And relationships between animals have similar characteristics, though these have so far been little studied. So for these reasons, I think it's becoming apparent that the analyses of social behavior, which depend on the isolation of the traditional categories of behavior, like feeding, flocking, and sexual behavior and so on, inevitably miss some of the most interesting problems. Now if I could have the next slide, please.

Now I want to say just a little bit about the structure of social groups. In the social groups of most primates and higher animals, each individual forms relationships with a number of other individuals. And each relationship may be based on one or more types of behavior: play, grooming, and sex and so on, and it may be either predominantly friendly or predominantly hostile. But the group is more than the sum of individual relationships. And if one is interested in the consequences of group living on the individual, one of the most important issues is the manner in which each relationship may be affected by others.

And as an example of this, I want just to consider for a moment, the small captive groups of rhesus monkeys which we study in Cambridge. Each group consists of an adult male, two to four females and their young. And our main interest is in the development of the young and that's why I've put the infant in the center of the diagram. The infant may form relationships with the members of virtually all age-sex classes in the group. And the solid lines in this figure are meant to represent those relationships. The thickness of the lines corresponding very roughly with the amount of interaction in each case. Though, of course, this is a matter that varies with age and between individuals and so on. Now the discontinuous lines in the figure

show some of the ways in which the relationships affect each other. For instance, the mother may permit the infant's elder sibling and their own best friends, which, for example, consider the animal labeled as "peer's mother" here, the mother may permit them access to the infant, but deny access to other animals. So the mother's relationship with the sibling and the mother's relationship with the peer's mother affects the relationships of those animals with the infant. In order to protect the infant from other females, the mother may behave restrictively towards it. And so the relationship of the mother to the infant is both influenced by, and affects, the infant's and the mother's relationships to other females.

Since the male may intercede in disputes, and if he does so is likely to take the side of his own favorites within the group, the mother may have to be more restrictive in protecting the infant from some females than from others. So the male's relationships with the females affects the mother's relationships with those females, and with her own infant. And one can go on in this way almost indefinitely; all the lines on this diagram are actually lines that we have quantitative evidence for in our own groups. And they're only some of the possible ways in which one relationship may be affected by others. So the point I'm trying to make is that the infant lives in a complex social nexus, changing any part of which may have repercussions on all the others. And the group structure involves not merely relationships between individuals, but relationships between relationships.

Now, social behavior implies that the behavior of individual animals is influenced by that of others. And this in turn implies some system of signaling between individuals. And the nature of the social signals used in intraspecies communication has often been reviewed, and I don't want to say a great deal about it this evening, but I do want to pick out one or two points which I think are important in the present context. And the first is this: one must ask the question, what exactly does it mean to say that two individuals communicate with each other? And you may think it curious, but there has been considerable controversy and misunderstanding amongst students of animal behavior on this issue, and it's now become clear, I think, that this misunderstanding… Well, the controversy, really, has arisen from attempts to distinguish between behavior that is communicative and behavior that's merely social. And students of animal behavior and of human behavior have argued about this. And the reason that there's been a dispute, I think, depends on the fact that some research workers are interested in how signals are adapted for their signal function. Others are interested in how signals are directed, and others on how the group hangs together.

An evolutionary biologist who's interested in the evolution of social behavior is likely to focus on movements or structures which appear to have been adapted for their signal function in evolution. And these are, especially, the social releases which have been studied by Lorenz,

Tinbergen, and other ethologists. That is, the more or less conspicuous structures or movements which affect the behavior of other individuals, and I'm going to come back and talk about those in a moment or two. A communication engineer who's interested primarily in the mechanics of the links between individuals is likely to focus instead especially on those in which one individual intends to affect the behavior of other individuals. Now, "intends to" you can give a more precise definition, of course, the criterion that A *intends to* affect the behavior of B is whether A varies his manner, varies his behavior, in such a manner that an effect on the behavior of B is most likely to occur.

The distinction I'm pointing to is the distinction between the unconscious smile that one makes when one sees somebody one's pleased to see, and the smile one puts on in an effort to put someone at their ease, or perhaps for some more nefarious purpose. Well, actually, the distinction between the behavior of A which affects the behavior of B, and behavior of A which is intended or directed towards affecting the behavior of B, is an important one, but it's not quite so easy to make the distinction as it might seem at first sight. Because by this criterion, many social releases which have been adapted in evolution for a signal function would be ruled out; for instance, birds' song, which is broadcast and not directed towards affecting the behavior of any other particular individual, would not be communicative. And indeed, if intention to influence the behavior of another individual is taken as the criterion of communication, you'd probably agree that much human speech is non-communicatory. Nevertheless, as I say, the distinction is important, especially in the study of the development of relationships between individuals, and I shall return to it tomorrow night.

Finally, the sociobiologist who's interested in how a social structure hangs together, has got to take into account every change in the behavior of one individual which affects, or might affect, the behavior of another, and this includes mere presence of the first individual. So he starts to study communication by assessing whether or not the behavior of each individual is affected by each aspect of the behavior of others. And the list of signals which he comes up with is likely to be a long one. So, as you can see on the table, the interests of these three hypothetical research workers overlap, but they're not coextensive.

Well, now let's just consider for a moment or two signals which have been adapted in evolution for a signal function. Many of these social releases appear in conflict situations. That is, they appear when the animal has incompatible tendencies to behave in more than one way. This figure is one of Tinbergen's pictures, and it shows a threatening herring gull. Now in fighting, the herring gull has two techniques, he pecks down on his rival, and he beats at his rival with his wings. In this slide, you see two forms of this upright threat posture of the herring gull; the upper one is very likely to lead into an attack, and you see that the beak is already pointing

downwards and the wings are already lifted out of their supporting feathers. The lower one is very likely to lead to withdrawal, and both these components are absent. And it's this variability in the threat posture that is one of the sources of evidence that the displaying bird is subject to conflicting tendencies to attack and to flee from his rival. This next picture shows a threatening rhesus monkey. And you can see that there again, the animal is in a conflict situation, it's actually trying to walk forward with its back legs and backwards with its front legs.

[laughter]

In general, if an individual is going to attack, or is going to flee, then its behavior is most likely to be effective if it does so directly, without signaling its intention. But if it may do either one or the other, and which it does depends on the behavior it's threatening, then signaling is essential. Well, comparative study of closely related species has shown that such signal movements, given in conflict situations, have very often evolved from one of two sources. Some come from intention movements. By intention movements, I mean the initial preparatory phases of a movement or a movement sequence. On the right here you see in diagrammatic form the intention movements of taking off by a bird. The bird first crouches, as shown on the left, and then straightens out and springs off. And on the left, you see three display movements, which have been evolved from these intention movements of taking off. You see, the components of taking off are there, but the relations between the components are changed, and the components are exaggerated.

Other signal movements have evolved from what students of animal behavior call "displacement activities," that is, from movements which are apparently irrelevant in the context in which they occur. Such as the hasty preening or grooming movements, which are often made by animals subject to incompatible conflicting tendencies.

Now this doesn't mean that all signal movements are derived from one of these two sources, or indeed that all signal movements are associated with conflict situations. But whatever their source, the movements have become changed in evolution to make them more effective for their signal function. Usually, this has involved increased conspicuousness, often increased differentiation from other movements of the same species, and often the development of conspicuous structures which accentuate the movement. And often the evolution of the movement and of the conspicuous structure have proceeded in parallel.

These are two European birds which are closely related to your chickadees, the great tit and the blue tit, they're the same genus. And throughout this genus, nearly all species—and this includes your chickadees—use an upright threat posture, like you see on the left. And the

degree to which this posture is accentuated is correlated with the degree to which conspicuous ventral structures have evolved, which this posture shows off; or, to put it the other way around, which accentuate the posture. The great tit has the most elaborate threat posture of this sort; it sometimes stands in that position craning its head upwards for several seconds at a time, and the black ventral stripe contrasts with the yellow breast. The blue tit on the right has practically no posture of this sort; occasionally I think I can see it, but very rarely. And when it's fighting it uses a head forward posture, as you see in this slide. And the blue tit, unlike any other members of the genus, can raise its cheek feathers to make this head forward posture conspicuous. And the raising of the cheek feathers goes just as far back as the boundary between the white and the black on the head. So there's a correlation between the evolution of the posture and of the structure.

Now, one can distinguish two ways in which movements have become specialized for a signal function. In some cases, the signal has become rigid and stereotyped, which presumably means that it's easy to interpret. In other cases the signal is graded, each point on a continuum corresponding to a particular motivational state. And such a signal is of course able to carry a lot of information, but it's more difficult to interpret. A classic example of the stereotyping of a signal movement which illustrates both of these points is shown here; this is another slide of Tinbergen's and concerns another gull species, the black-headed gull. And this particular posture… well, two postures are shown here, the oblique and the forward, they're both associated with slightly different motivational states; I should add that the motivational state is assessed in terms of what follows the posture. And there are intermediates between these two postures, but the intermediates are very rare. Well now, since the motivational state presumably fluctuates over a continuous range, but the posture over a more or less discontinuous one, it seems as though the posture has become, as it were, concentrated on two points in its continuum, each of which corresponds to a range of motivational states.

The fact that there are graded signals and there are rare intermediates between discrete signals, and the fact that in any case, not all social communication depends on these social releases which have been adapted in evolution for a signal function, makes it very difficult to assess how big the repertoire of signal movements of any one species is. And I think that although you'll see figures in the literature, I think absolutely no significance is to be attached to them whatever. But it's of the order of thirty. It's not very large for most species of mammals and birds which have been investigated. And that raises the question of how the complex social life of many of these species can be maintained if they possess such a small number of discrete signals. Surely, you would think that the diversity of things which must be signaled must be much greater than this relatively small repertoire would allow.

Well, there are two points here. One is that many of the postures listed in descriptions of communicatory behavior are in fact combinations of more elemental components. Sorry, I messed that one up. This is a picture of two tits threatening each other over a milk bottle, and the right-hand bird is showing three things I'll call your attention to: its wings are raised, its nape feathers are raised, and its tail is slightly spread. Well, a detailed study of the agonistic behavior of this bird at a winter feeding station was made by Professor Stokes, and he recorded nine behavioral components, like crest up or down, wings raised or down, and so on, and the subsequent action of the posturing bird, which he classified as either attacking, staying, or fleeing. And the association between the individual components and the subsequent behavior of the bird was usually not very large. The component which had the best association with attack was a horizontal body, but that was only followed by attack in 40% of the cases in which it appeared. The best one was escape, which followed an erect crest in 90%, but you can see that neither attacking nor staying could be very well predicted from any one component.

Now, this lack of predictability was in part due to interaction between the components. If you look at the bottom three double lines in this table, these are all non-aggressive postures. And in each case, the top line refers to a situation in which the nape feathers are erected, and the bottom line to a situation in which they're not. And you'll see that in each of these non-aggressive postures, the raising of the nape feathers results in an increased probability of attack. 32 to 6, 43 to 12, and 41 to 17. But in the top two lines, you see aggressive postures. And in those cases, the raising of the nape feathers either results in no difference, or if anything, a decrease in the probability of attack. And means an increase in the probability that the bird will stay. So that the significance of any one component varies with the other components which it accompanies.

Combinations of components show somewhat more reliable relationships with subsequent behavior. If you look at the plus and minus table on the left, you can see each line represents a combination of components. And you will see that there is one line… the top line is followed by escape in 94% of cases, and this is slightly better than the 90% you get with single components. And you see on the right that the third line down is followed by staying in 79% of cases, and this is considerably better than the 52% you get with single components. So if you use multiple components, you can get more subtle indications of what the bird is going to do, and more reliable predictions. But in no case is the prediction perfect. And I think that this could be in part because the human observer is not able to see the subtleties in the posture, but I think it's also probably due to the dependence of what the displaying bird does on what its rival does.

Now, I want to turn to a second reason why this relatively limited vocabulary of animals is more effective than you might think at first sight. Here, we've seen that the significance of any one

component depends on the context of other components in which it occurs. And the same is true for the signal movement as a whole. The actual display posture itself is only part of the information which is available to a recipient. Because each signal is made in a context, and that context is an essential clue to the interpretation of the message.

One of the best examples here comes from the studies of tyrannid flycatchers by a man called Smith, and I'm just going to cite one of the examples that he gives. He describes a vocalization which he calls the "locomotory hesitance vocalization," it's just a little brief note, much shorter than the label which he's given it. It's given in a wide variety of contexts, and the common feature in those contexts seems to be that the calling bird is in a conflict between locomotion and some other type of behavior. Now, the response to this vocalization varies with the recipient and the context. So that the caller's mate nearly always merely replies with the same call. But if the caller is a patrolling male, an unpaired female is likely to approach, but another territorially inclined male may either approach aggressively or withdraw, and a migrating individual will probably avoid the caller altogether. So that a single call, which occurs in a wide variety of situations, can induce diverse responses depending on the context and the motivational state of the recipient.

Now, for such reasons as these, the communicatory systems of animals are much more effective than might appear at first sight from the number of signals they contain. We must ask, therefore, whether they ever approach the effectiveness of human speech. Well, of the attempts to assess the relationships between the communication systems of animals and that of man, the most effective is that of Hockett and Altman. And what they did was to specify certain design features of human speech, and to see whether the communicatory systems of animals possess those design features. They actually specified sixteen design features of human communication, but I just put up four in the slide.

Human language involves symbols, which are abstract or arbitrary in that they do not resemble, in physical contours, that to which they refer. Human speech is based on discrete signals; it can refer to events remote in time and space, and it's open in the sense that new messages can be coined freely and easily. Well, you can ask, for instance, whether these design features are possessed by the well-known dance by which worker honeybees can communicate to other worker honeybees the location of a new food source. The bees do this by dancing on the hive, and the direction of the dance is physically related to the direction of the food source. And it also… the direction of the dance varies continuously. So the symbols cannot be said to be either arbitrary or discrete. In only a very limited sense can the dance be said to permit the coining of new messages. But it does refer to a food source that is remote in space.

By contrast, to take another example, the auditory communication of doves does involve discrete and arbitrary signals, but it's not open, and it can't refer to things remote in time and space. So that in this sort of way, you can assess the extent to which the communication systems of different species share design features with each other, and with human language. However, for comparisons between the systems of man and animals, I think that this design features approach has a somewhat limited value, because the interpretation of the design features is somewhat flexible. It is argued, for instance, by Thorpe, that the bee dance is open, because the worker bee can report a location which has never been reported before. But this is surely a very limited sort of openness, for the bee dance communicates only about the location of new nectar and hive sites, and it's confusing to say that bee dance shares a property of openness with human language. But I think actually that it's of course quite clear that no subhuman system of communication comes anywhere near approaching the complexity of human language.

However, we've got to remember that we communicate with each other not only by words; we gain a great deal of information from the postures, gestures, facial expressions and intonations of those with whom we come into contact. And it is beginning to become apparent that these nonverbal communicatory gestures have links on the one hand with those used by subhuman species, and are also, in other ways, quite closely related to verbal language. Now I want to say a few words about these.

Certain movement patterns are common to all human cultures so far investigated. Smiling, crying, laughing, and so on. And some of these we're not even conscious of when we use them. For instance, Eibl-Eibesfeldt has recently described the eyebrow flash, a very rapid raising and lowering of the eyebrows, which is used in greeting in all cultures which he has so far looked at. Now, this eyebrow flash had never been described before, two or three years ago. And as a matter of fact, I first heard him describe this at a conference held in France two or three years ago, and for the whole of the rest of the conference it was quite impossible for anybody there to say hello to each other.

[laughter]

They immediately became conscious that they had used, subconsciously, a gesture which, had they used it deliberately, would have been interpreted as flirting. Many of these sorts of gestures appear in deaf and blind-born children, making it very unlikely that imitation or learning from others is important in their development. And furthermore, comparative studies are beginning to permit reasonable hypotheses about the way in which they've evolved. A Dutchman, van Hooff, has recently used a wealth of comparative observational and

experimental evidence to study the relationship between smiling and laughing. And he believes that these constitute a continuum of integrating signals, most of the variation on which you can understand in two dimensions, which you can describe roughly as friendliness and playfulness. Well now, two extreme forms, which he calls the broad smile and the wide mouth laugh, which is shown on the left and the right at the bottom here—it's not a very good picture of a broad smile, I don't think—you can trace, from the silent bared teeth display, and the relaxed open mouth display of lower primates. The evolution of the silent bared teeth display, which is a gesture made in fear by lower primates, you see on the left, and the relaxed open mouth display on the right. And these two have come together in the apes, and hence you see the sort of picture of the evolution of human smiling and laughter at the bottom. Now, I don't want to go along with any of the details of this diagram. The point I'm trying to make is that an evolutionary understanding of many of these expressive movements is at least possible.

Now, certain syndromes of behavior are also remarkably similar between cultures. Anger, for instance, involves particular facial expressions, waving the arms, stamping the ground, and so on. And it's quite humiliating to watch an angry chimpanzee; you'll find that he does exactly the same. In many of these cases, not only the motor patterns themselves, but also the motivational basis of the movements, are similar between individuals and between cultures. But these aspects are more labile than the movement pattern itself. And there may be differences between cultures, in that a movement pattern may be used in a wider range of contexts in one culture than in another, or it may even be entirely suppressed. The eyebrow flash, which I referred to just now, is considered indecent and is suppressed in Japan, but in Samoa it's used in greeting and also as a sign of approval or agreement when seeking confirmation in a variety of other contexts. And furthermore, some of these expressive movements have special uses in particular cultures, for instance there are cultures in which laughing is used in mourning.

Now similarities between cultures are especially likely with signals which concern personal or emotional characteristics, whereas you are most likely to get differences between cultures in movements which substitute for verbal communication. And I would emphasize that the diversity to be found between cultures in gestures of affection, greeting, and so on, is very great indeed.

The greatest diversity of all between cultures you get in acts of nonverbal communication which symbolize aspects of the culture which depend on verbal language, or which have cultural implications at more than one level of complexity. Now, to exemplify some of the problems posed by human nonverbal communication—and in case any of you think that I've been oversimplifying—I'm going to show two pictures. And these two pictures were both taken with

an old-fashioned camera on a tripod around the turn of the century. They were first shown to me by Cambridge anthropologist Edmund Leach. And in the two pictures, the hand posture is identical in both cases. And when you look at them, I want you to think, first of all, whether the similarity between the two is merely coincidental, or whether it's meaningful; and second, whether your interpretation of the meaning of the posture depends on the context, as shown by the picture, or on your own preconceptions or preoccupations. The first slide is of Proust's mother. And notice the way she holds her hand. And the second is a picture taken by the anthropologist Radcliffe-Brown of an Andaman Islander.

Well now, so far we've been concerned with the nature of social behavior, and in the last few minutes, I want to say a word or two about development. Development is a continuous process, and it involves an ongoing interaction between the organism and its environment. And if we're to understand the course of development, we've got somehow to tease apart the processes involved in that interaction. In the past, it's been customary to divide behavior into that which is instinctive, innate, inborn, or genetically determined, or something of that sort, and, on the other hand, that which is learned or acquired. And I want to point to you that as far as understanding the processes of development goes, such a dichotomy of types of behavior is both false and sterile.

Let's consider two simple non-social patterns of behavior first. In Europe, as in North America, there are a number of species of seed-eating finches. And the species differ in the size of their beaks, and also in the seeds which they select to eat. And it used to be said that beak sizes had become adapted to the size of the seed which the species instinctively selected. But studies showed that individual experience plays a very large role in determining the size of seeds selected. One aspect of this being that individuals tend to learn to select those seeds which they can open most efficiently with the beaks that they've got. And by most efficiently, I mean that they can obtain maximum kernel weight per time spent opening. So individuals of the species tend to have similar seed preferences because they have similar beaks. Seed preference is not instinctive or innate, but is in part a product of experience; the species' constancy being determined by the morphological similarity of the individual. Now as a second example, tits or chickadees often open seeds by holding the seed by their foot against the perch, and then hammering at it with their beak. All members of the genus *Parus* can hold seeds in this way, but many other seed-eating birds cannot. We reared chaffinches, which is a European finch, and we even allowed chaffinches to be reared in tits' nests by tits, but chaffinches never ever hold seeds in this way.

Well, although all tits can hold seeds in this way, hand-reared birds, if you watch them closely, have to learn to do it. They go through a phase of learning to place the seed under the foot.

And if you rear them without adequate opportunity, or with restricted opportunity to play with seeds, the age at which they perfect this depends on the amount of opportunity they've had for practice. Well, what conclusions can one draw from these two experiments? What one can say is, that the differences between goldfinches and chaffinches, or the differences between chaffinches and tits in their ability to use the foot are innate or genetically determined. For in each case, individuals of the two species reared in the same environment, come to behave differently. Since the environments are identical, the differences must reside in the genes, this is shown on the bottom line here. But in neither case can we say that the behavioral character is innate or genetically determined, if that implies that it develops independently of experience.

In another type of experiment shown on the top line here, one could vary experience while keeping genetic factors constant, by using identical twins or groups drawn from the same population. And any differences which then appeared could be ascribed to the differences in experience. But of course, this would not mean that the genetic constitution is not important,\; it would still be one of the important determinants of how the animals respond to the different environments. So from evidence of this sort, it can be argued that the most useful questions about development concern not the nature of characters, but the sources of differences between characters. And the conclusions from any experiment or controlled observation of behavior reduce, ultimately, to conclusions about differences. Now, just to turn to a slightly more complex case involving a signal that's used in social communication: bird song, and I'm going to talk only about once species, the chaffinch.

Each individual male chaffinch produces, in its first spring, a small repertoire of song types, of the types shown in the upper of these two pictures here. These are sound spectrographs which are graphs of frequency against time. Now, you'll see that it's a fairly complicated song. Now, if you rear chaffinches in isolation from other chaffinches, so that they never hear the song of adult chaffinches, they produce only a very simple song type of the type shown in the bottom graph, not differentiated into phrases and lacking much of the complexity of the normal song. So the difference between the simple song produced by these birds reared in isolation and the normal song can be ascribed to experience. The next question is how this experience operates. Birds which hear song in their first autumn before they themselves start to sing, and kept subsequently in auditory isolation, sing a song more like normal song than birds reared in isolation. Here are… the normal birds get some exposure to song when in their early weeks, and some in their first breeding season. The isolate that I was speaking about gets perhaps…

[audio cuts out; resumes briefly after]

So that it corresponds to what they have learned that the song should be like.

However, chaffinches won't learn any song which they hear. From all the songs which they hear, either in their first spring or their first autumn, they learn to model their own song on those songs which resemble, in note structure, normal chaffinch song. So that they will learn a chaffinch song with the end transposed to the middle, but they will not learn the most perfect representation that we could make of a chaffinch song on a very beautiful 17th-century college organ. Because the notes were pure notes. And so for this reason, they won't learn the songs of alien species.

Well, such facts, based on experiments between groups of birds treated in different ways, can be integrated on the view that chaffinches first learn what to sing and then learn how to sing it. And this leads to two predictions; one is that in learning how to produce the song pattern which it's acquired, the chaffinch monitors its own output, and repeats utterances which approximate to the song that it's previously heard. And one can predict from that that hearing the correct song should be reinforcing. And second, you can predict that if you deafen it between when it heard the model and when it starts to sing itself, its song learning should be prevented. And both of these predictions are in fact true.

Well, this is only a very brief summary of quite a lot of work which has gone on on song learning in the chaffinch, but I think it suffices to illustrate that the song develops as a result of a very complex interaction between the bird and its auditory environment, over a long period. We can say that chaffinches differ from other species in the sorts of songs they'll learn to sing, or in the song they produce if kept in isolation. But even the song produced by birds kept in isolation from soon after hatching cannot properly be described as innate, for it's also affected by deafening. And even deafening at an early age removes only some of the effects of experience; the amorphous sequence of notes which is in fact produced by such birds still depends on many as-yet unanalyzed aspects of experience, as well as on the genetic constitution.

Well, that's something about the development of a relatively simple pattern, which depends on an interaction between the bird or the animal and its environment. Now, tomorrow night I'm going to talk about the development of social behavior, and this depends on an interaction not between the organism and an inanimate physical environment, but between two behaving organisms. And therefore the task of teasing apart the processes involved in the development of social behavior is even more complex. And I shall be discussing, in some detail, only the behavior of rhesus monkeys and the relevance of that behavior to man. Thank you.

[applause]

HOST: Thank you very much, Dr. Hinde. This, of course, concludes the formal lecture for this evening. I remind you of the lecture again tomorrow evening, the continuation lecture tomorrow evening. For those of you who have questions, Dr. Hinde has very generously agreed to respond to them and I would ask you if you do, for those of you who do, if you would please come forward and he will informally respond to the questions that you have. Thank you very much.

[program ends]

[*Note: Dr. Hinde's second lecture the following evening was recorded, but damage to the tape prevented playback and it could not be transferred.*]